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Invariant Gametogenic Response of Dominant Infaunal Bivalves From the Arctic Under Ambient and Near-Future Climate Change Conditions

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Arctic marine ecosystems are undergoing a series of major rapid adjustments to the regional amplification of climate change, but there is a paucity of knowledge about how changing environmental conditions might affect reproductive cycles of seafloor organisms. Shifts in species reproductive ecology may influence their entire life-cycle, and, ultimately, determine the persistence and distribution of taxa. Here, we investigate whether the combined effects of warming and ocean acidification based on near-future climate change projections affects the reproductive processes in benthic bivalves (*Astarte crenata* and *Bathyarca glacialis*) from the Barents Sea. Both species present large oocytes indicative of lecithotrophic or direct larval development after ∼4 months exposure to ambient [<2°C, ∼400 ppm (CO_2)] and near-future [3–5°C, ∼550 ppm (CO_2)] conditions, but we find no evidence that the combined effects of acidification and warming affect the size frequency distribution of oocytes. Whilst our observations are indicative of resilience of this reproductive stage to global changes, we also highlight that the successful progression of gametogenesis under standard laboratory conditions does not necessarily mean that successful development and recruitment will occur in the natural environment. This is because the metabolic costs of changing environmental conditions are likely to be offset by, as is common practice in laboratory experiments, feeding *ad libitum*. We discuss our findings in the context of changing food availability in the Arctic and conclude that, if we are to establish the vulnerability of species and ecosystems, there is a need for holistic approaches that incorporate multiple system responses to change.

Keywords: metabolic plasticity, functional response, oogenesis, life-history, dynamic energy-budget

INTRODUCTION

Ocean acidification and warming are synergistic environmental stressors (Byrne et al., 2013a) that can affect whole animal physiology (Pörtner and Farrell, 2008). However, the extent to which reproduction and life history strategy are vulnerable to environmental change has received comparatively little attention (Ross et al., 2011). Reproduction underpins the success of populations

over time and, regardless of parental survivorship and tolerance capability, negative species responses to novel circumstances at early life cycle stages have the potential to serve as a bottleneck to long-term population survival (Dupont et al., 2010a). Species responses to changing environmental conditions have been shown to carry a high energetic cost in marine calcifiers (Spalding et al., 2017), especially at higher latitudes (Watson et al., 2017), and at earlier stages in the life cycle (Ross et al., 2011; Foo and Byrne, 2017). This is particularly concerning in polar environments where species responses to global climate change and ocean acidification are widely considered to be regionally amplified (Miller et al., 2010). Discerning the direction and generality of effect, however, is frustrated by the effects of transgenerational plasticity (Karelitz et al., 2019; Kong et al., 2019; Byrne and Hernández, 2020; Byrne et al., 2020), as well as intra-specific variations in sensitivity (Przeslawski et al., 2015) and response (Carr et al., 2006; Campbell et al., 2016; Boulais et al., 2017). In addition, maternal environmental history has been shown to affect egg size and volume (Braun et al., 2013) which, in turn, can induce phenotypic responses in larvae (Byrne et al., 2020).

Overall, the combined effects of ocean acidification and temperature on early gamete development are poorly constrained (Boulais et al., 2017) with most available information focused on gamete viability post spawning or larval development in a limited number of taxonomic groups (see review by Ross et al., 2011 and meta-analysis by Kroeker et al., 2010). By focusing on the later stages of a species reproductive cycle, sensitivities of gametogenesis or fertilization mechanisms are missed, stimulating debate about the potential for reproductive cycles to be disrupted (Dupont et al., 2010a; Hendriks and Duarte, 2010). Indeed, empirical evidence for the echinoderms indicates that ocean acidification can result in delayed but normal gametogenesis (Kurihara et al., 2013), reduced sperm volumes (Uthicke et al., 2013), lower gonad indices (Stumpp et al., 2012), or smaller eggs (Suckling et al., 2015). However, experimental manipulation of acidification in other taxa, including corals (Jokiel et al., 2008; Gizzi et al., 2017), annelids (Gibbin et al., 2017), molluscs (Parker et al., 2017), crustaceans (Thor and Dupont, 2015), and several miscellaneous species (for comprehensive list see Foo and Byrne, 2017), reveal no effects on egg size, gametogenesis, or development. Hence, considerable uncertainty exists in understanding the impact of climatic forcing on individual species within the context of the wider ecosystem, but it is clear that the earliest stages of gamete development need to be considered whilst adequately addressing variations within populations and regional environmental change (Dupont and Pörtner, 2013).

While many regionally abundant benthic invertebrate species have shown physiological tolerance to environmental forcing, often explained by, or attributed to, their boreal evolutionary histories (Richard et al., 2012), the viability of Arctic populations through their ability to reproduce is not currently known. Here, we used two abundant and functionally important benthic bivalves, *Bathyarca glacialis* and *Astarte crenata* from the Barents Sea (Cochrane et al., 2009; Solan et al., 2020), a region undergoing rapid change including ice retreat (Polyakov et al., 2012a), increasing sea surface temperatures (Polyakov et al., 2012b), and ocean acidification (Qi et al., 2017), to examine the combined effects of warming and ocean acidification on gamete development. Both species are reported to have large oocytes all year round indicative of lecithotrophic or direct development, and without seasonal or cyclic patterns of oocyte development (Saleuddin, 1965; Von Oertzen, 1972; Oliver et al., 1980). Our *a priori* expectation was that the physiological cost of near future conditions would indirectly affect reproduction, expressed via a trade-off with egg size or increased oocyte reabsorption, with consequences for the long-term viability of the population.

METHODS

Specimens of the infaunal bivalves *Bathyarca glacialis* and *Astarte crenata* were collected in July 2017 and 2018, respectively, by Agassiz trawl in the Barents Sea (74–81°N, along 30°E meridian, 292–363 m depth, JR16006 and JR17007, *RRS James Clark Ross*, **Supplementary Table 1**). Similarly sized individuals of each species (**Supplementary Table 2**) were maintained in aerated seawater (salinity 35, 1.5 ± 0.5°C), and returned to the *Biodiversity and Ecosystem Futures Facility*, University of Southampton. Surficial sediment (less than 10 cm depth: year 2017, mean particle size = 28.06 μm, organic material, 6.74%; 2018, mean particle size = 26.51 μm, organic material, 6.21%; Solan et al., 2020, **Supplementary Table 3** and **Supplementary Figure 1**) was collected using SMBA box cores in the Barents Sea (year 2017, Station B13, 74.4998°N 29.9982°E, 346 m depth; year 2018, Station B16, 80.1167°N 30.0683°E, 280 m depth, and Station B17, 81.2816°N, 29.3269°E, 334 m depth), sieved to remove macrofauna (500 μm mesh), homogenized by stirring, and transported back to the University of Southampton at ambient temperature (1.5 ± 1°C).

We exposed individuals of *Bathyarca glacialis* and *Astarte crenata* to ambient [1–2°C, ∼400 ppm (CO_2)] and near-future [3–5°C, ∼550 ppm (CO_2)] based on IPCC RCP 4.5 and 6.0 future projections for around the year 2050–2080, IPCC, 2013) temperature and atmospheric carbon dioxide scenarios for the Barents Sea. Aquaria (L × W × H: 20 cm × 20 cm × 34 cm, transparent acrylic) were continually aerated by bubbling a treatment-specific air-CO_2 mixture through a glass pipette (Godbold and Solan, 2013) and were filled with 10 cm of homogenized sediment overlain by 20 cm of seawater (∼ 8 L, salinity 34). The aquaria were maintained in the dark and randomly distributed between two insulated water baths within each treatment (Solan et al., 2020). Three *B. glacialis* were introduced to each of twelve aquaria (n = 36) and six *A. crenata* were introduced to each of ten aquaria (n = 60). After acclimation to aquarium conditions at ambient temperature and CO_2 [30 days, 1–2°C, ∼400 ppm (CO_2)], temperature and (CO_2) were adjusted manually (1°C and ∼100 ppm CO_2 week^{-1}) to achieve the near-future treatment conditions. No mortality was recorded during this period. We periodically measured pH [NBS scale, Mettler-Toledo (United States) InLab Expert Pro temperature–pH combination electrode], temperature and salinity (Mettler-Toledo InLab 737 IP67 temperature–conductivity combination

electrode), and total alkalinity (HCl titration by Marianda VINDTA, Canada). Concentrations of bicarbonate (HCO_3^-), carbonate (CO_3^{2-}), and pCO_2 were calculated from measured pH, total alkalinity, temperature, and salinity (Dickson et al., 2007; Dickson, 2010) using CO_2calc (Robbins et al., 2010) with appropriate solubility constants (Mehrbach et al., 1973, refit by Dickson and Millero, 1987) and KSO_4 (Dickson, 1990; **Supplementary Figures 2**, **3**).

The bivalves were fed consistently throughout the acclimation and experiment period *ad libitum* three times per week with 100 ml cultured live phytoplankton (mixed *Isochrysis* sp., *Tetraselmis* sp., and *Phaeodactylum* sp.) at peak culture densities of 15.6×10^6 cells ml^{-1}, 8.6×10^5 cells ml^{-1}, and 14.2×10^6 cells ml^{-1}, respectively. This equates to ∼0.197 g algae per day and represents 9.93 and 6.42% of algal weight/bivalve wet mass in *Astarte* and *Bathyarca*, respectively. Uneaten food was observed settled on the sediment surface which was used as an indicator of feeding *ad libitum*, and overlying sea water was replaced weekly (partial exchange, ∼80%) to prevent the accumulation of excess nutrients. Experiments were run for 120 days (*B. glacialis*, 21/11/2017–20/03/2018) or 135 days (*A. crenata*, 8/10/2018 – 19/02/2019) after which animals were removed and fixed in 4% neutral buffered formaldehyde for approximately 1 month before being prepared for histological examination. No premature mortality was recorded.

Histology

Bivalves were selected for histology within a defined size range (*A. crenata* 25–30 mm shell length; *B. glacialis* 20–25 mm shell length). For each individual [*A. crenata*, $n = 37$ (19 ambient, 18 future); *B. glacialis*, $n = 24$ (12 ambient, 12 future)], maximum shell length, height, and tumidity were measured using a digital caliper (±0.01 mm) (**Supplementary Table 2**), before soft tissue was removed from the shell, wet weighed (±0.001 g), and prepared for histology. Dissection revealed that both species have gonads which infiltrate and partially envelop the digestive diverticula (**Figure 1A**) so, as it was not tractable to perform a dissection of the germinal tissue, we adopted whole animal histology for reproductive analysis.

Soft tissue of each specimen was processed for histology according to the protocols described by Lau et al. (2018). In brief, tissue was dehydrated in isopropanol (70–100%), cleared in XTF (CellPath Ltd., United Kingdom) and embedded in 25 mm × 50 mm paraffin wax blocks. Embedded tissue was cut at 6–7 μm, mounted onto slides and stained using hematoxylin Z (CellPath Ltd., United Kingdom), counter stained with eosin Y (CellPath, United Kingdom), and immediately cover-slipped using a DPX mounting medium (Sigma-Aldrich, United Kingdom). Oocytes were captured using a Nikon D5000 digital SLR camera mounted onto an Olympus (BH-2) stereomicroscope and analyzed using ImageJ v 1.48 (Schneider et al., 2012).

Unique oocytes were measured only when a nucleus was visible to ensure the near maximum cross sectional diameter. The size of each oocyte was standardized to the diameter of a circle with an equal aggregate sectional area to the two dimensional section of the imaged oocyte [Equivalent Circular Diameter (ECD), Lau et al., 2018], comparable to the Oocyte Feret Diameter used in previous studies (Higgs et al., 2009; Reed et al., 2014). For each female with more than 100 sectioned oocytes, we calculated the ECD of 100 oocytes in each female (five females and 500 oocytes per treatment in each species). A Chi-squared test of independence was conducted between individual females in each experiment treatment to determine a statistically significant association in oocyte size frequencies (**Supplementary Figures 4**, **5**). Oocyte length frequency distributions for each treatment were pooled to represent the natural variation within individuals, and were analyzed with a Kolmogorov–Smirnov (K–S) test between treatments. All analyses were conducted in R (R Core Team, 2018 v.1.2.5019) and the *fishmethods* library was used for analysis of the length frequency distribution and K–S test (Nelson, 2019).

RESULTS

Examination of the reproductive organs of *A. crenata* confirmed 16 females and 21 males with no evidence of hermaphroditism, and one specimen with no discernible gonad tissue. Oocytes were developing in reproductive organs infiltrating the digestive diverticula (**Figure 1A**) and consisted of interconnected gonadal alveoli (**Figures 1B,C**). In four specimens in the future climate treatment, oocytes were loosely held within the supra-branchial chamber and reproductive organs simultaneously (**Figure 1D**). Evidence of primary oogenesis was not observed, however, oocytes measured between 46.96 and 185.08 μm (mean ± SD 122.61 ± 22.84 μm, $n = 500$) in the ambient conditions (**Figure 2A**), and 44.61–181.93 μm (mean ± SD 122.48 ± 24.08, $n = 500$) in the future conditions (**Figure 2B**), with no notable evidence of atresia. The oocyte size distributions were not treatment specific (2-tailed K–S test, $D_{(116)} = 0.062$, $p = 0.99$), and showed a distributional peak between 100 and 150 μm.

Histological examination of reproductive organs of *B. glacialis* revealed 10 females and 14 males with no evidence of hermaphroditism. Gonads were positioned partially infiltrating the digestive diverticula (**Figure 3A**) and were observed in densely packed anterior-posterior tubular pouches up to six oocytes across (**Figures 3A,B**). Oocytes measured between 39.60 and 144.77 μm (mean ± SD 96.77 ± 14.36 μm, $n = 500$) in the ambient conditions, and 35.07–144.90 μm (mean ± SD 95.03 ± 18.57 μm, $n = 500$) in the future conditions, with no notable evidence of atresia. The oocyte size distributions were not treatment specific (2-tailed K–S test, $D_{(94)} = 0.122$, $p = 0.81$), but showed a peak at 85 μm following exposure to ambient conditions (**Figure 4A**) and 95 μm following exposure to future conditions (**Figure 4B**).

DISCUSSION

We have demonstrated, for two abundant species of Arctic-boreal bivalve, evidence of gametogenic resilience to projected near-future atmospheric carbon dioxide (550 ppm CO_2) and sea temperature (+3°C), after a 20 week incubation. Our

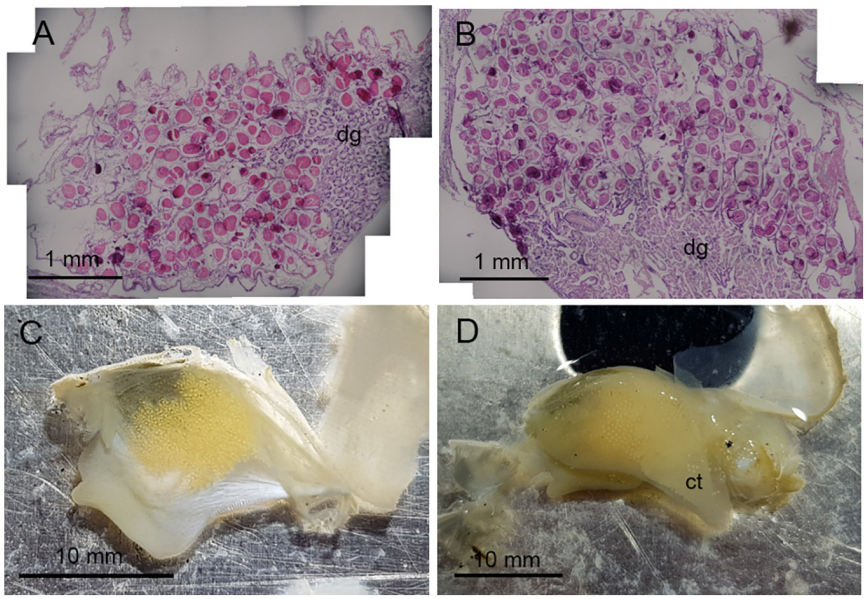

FIGURE 1 | Oocyte development in *Astarte crenata* from the Barents Sea. Transverse histology sections show oocyte development **(A)** surrounding the digestive diverticula under ambient environmental conditions and **(B)** in the gonadal alveoli under representative future environmental conditions. Microphotographs show **(C)** the arrangement of oocytes when within the gonad and **(D)** oocytes loosely held within the supra-branchial chamber on the ctenidia found in the future environmental conditions. dg, digestive diverticula; ct, ctenidia.

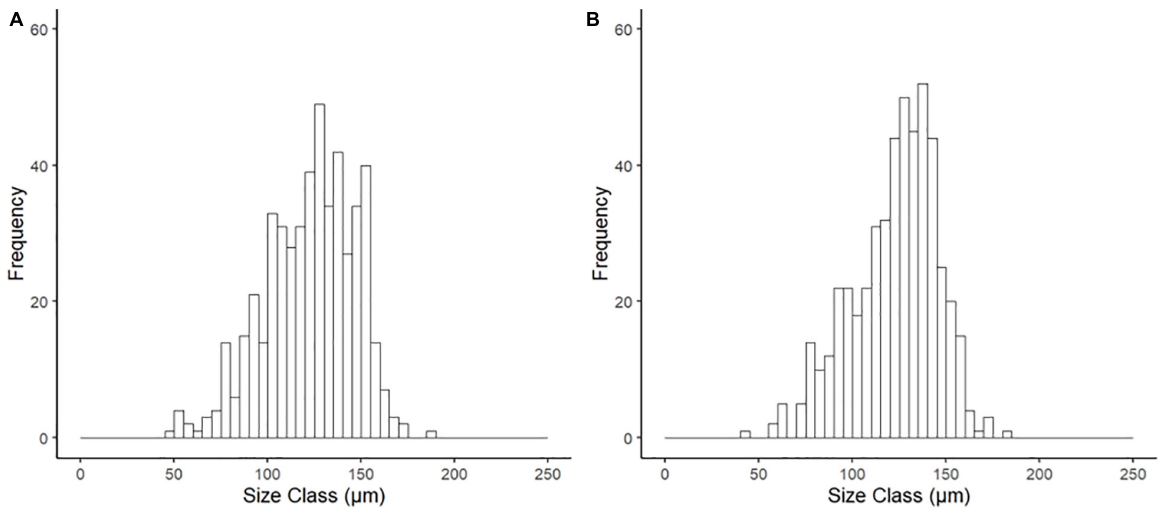

FIGURE 2 | Size frequency of oocytes for *Astarte crenata* from the Barents Sea following incubation (20 weeks) under **(A)** ambient and **(B)** representative future climate conditions. There was no difference in distribution between treatments (2-tailed *K–S* test, $D_{(116)} = 0.062$, $p = 0.99$).

observations show no difference in oocyte size frequency or physical structure, and in this respect are consistent with other studies (Kurihara et al., 2013; Verkaik et al., 2017). However, the interpretation of reproductive resilience based on a gametogenic response risks the generalization of a fundamental physiological output impacting on population dynamics, and does not take into account prolonged developmental cycles in cold water (Peck, 2016; Moran et al., 2019), or the effects on viability, fertilization, and larval development (Dupont et al., 2010a). The maximum oocyte sizes in *A. crenata* and *B. glacialis* are slightly lower than those reported previously (∼200 and 170 µm, respectively, Von Oertzen, 1972; Oliver et al., 1980; see **Supplementary Table 4**), likely representing different stages of maturity, and are consistent with the current understanding of reproduction in these species. Both species have egg sizes which suggest direct development or short pelagic development (i.e., lecithotrophic) (Ockelmann, 1965), and the small variation in oocyte frequency observed within treatments (**Supplementary Figures 4**, **5**) are

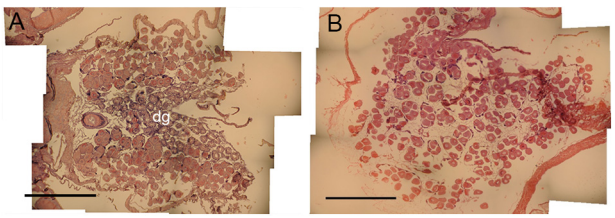

FIGURE 3 | Oocyte development in *Bathyarca glacialis* from the Barents Sea. Transverse histology sections show **(A)** reproductive organs and oocytes infiltrating the digestive diverticula under ambient environmental conditions and **(B)** oocyte development under representative future environmental conditions. dg, digestive diverticula. Scale bars = 1 mm.

akin to continuous spawners with an overlying seasonal intensity in reproduction (Lau et al., 2018), or natural variations in reproductive fitness. However, the presence of eggs in the suprabranchial chamber in four specimens of *A. crenata* exposed to future conditions is indicative of brooding, a previously unreported reproductive trait that is also supported by the large egg sizes, and formally hypothesized by the presence of adherent eggs and observed internal fertilization within Astartidae (Ockelmann, 1958; Marina et al., 2020).

It is tempting to conclude that our findings indicate resilience of the reproductive stage examined to near-term climatic forcing, but our observations of the successful progression of gametogenesis took place under standard laboratory conditions which, following accepted protocols (e.g., Pansch et al., 2018), include a constant supply of food. This may have inadvertently provided a sufficient supply of energy to overcome the metabolic costs of environmental stress (Cominassi et al., 2020) and mitigated the impact on gametogenesis. Increasing temperature and carbon dioxide concentrations affect species physiology through increased metabolism (Parker et al., 2013; Jager et al., 2016; Leung et al., 2020), and sometimes the suppression of feeding (Stumpp et al., 2012; Kurihara et al., 2013; Appelhans et al., 2014), which directly affects per offspring investment (Moran and McAlister, 2009; Pettersen et al., 2019), and gamete behavior post spawning (Verkaik et al., 2016). Energy stored as gametes can also be reabsorbed and act as a trade-off with fecundity (Stumpp et al., 2012; Verkaik et al., 2017; Rossin et al., 2019). However, considerable physiological resilience to ocean acidification has been demonstrated at various life-cycle stages in bivalves (Dell'Acqua et al., 2019), echinoderms (Verkaik et al., 2017), and corals (Gizzi et al., 2017), and during short incubations, appears to show no significant effects on growth and reproduction in benthic invertebrates (Dell'Acqua et al., 2019), even in food limited scenarios (Goethel et al., 2017). Laboratory experiments have shown that higher food quality and availability has a role in buffering the physiological effects of climate change and ocean acidification (Asnaghi et al., 2013), with positive effects reported in *Calanus* copepods (Pedersen et al., 2014), bivalves (Thomsen et al., 2013), and barnacles (Pansch et al., 2014). Further, a recent study has demonstrated that *ad libitum* feeding mediated fish growth rates in ocean acidification and warming scenarios, and suggest that this standard method may not reliably detect the impacts of environmental change in laboratory experiments (Cominassi et al., 2020). In our study, the supply of sufficient and nutrient rich food, common to laboratory experiments, is likely to have moderated the effects of near-future carbon dioxide and temperature controls (Thomsen et al., 2013; Ramajo et al., 2016; Cominassi et al., 2020), and provided the necessary nutrients for successful gamete development. Nevertheless, the physiological fitness of a species and production of gametes does not imply their viability, successful development, or recruitment to the environment (Caroselli et al., 2019).

Environmental change does not only have a direct physical effect on species physiology (Pörtner and Farrell, 2008), but also changes the wider ecosystem, including food-web structures

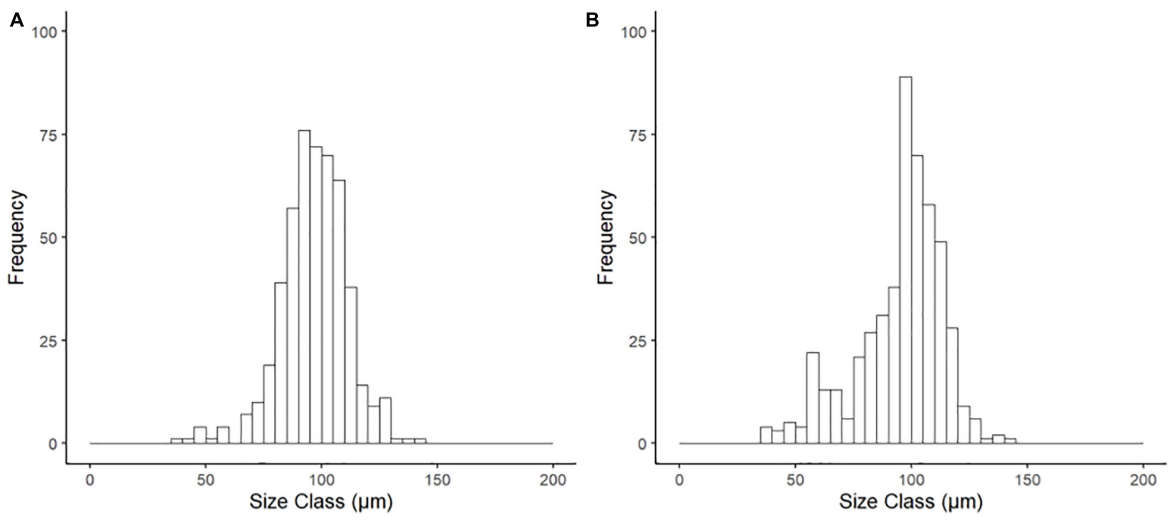

FIGURE 4 | Size frequency of oocytes for *Bathyarca glacialis* from the Barents Sea following incubation (20 weeks) under **(A)** ambient and **(B)** representative future climate conditions. There was no significant difference in distribution between treatments (2-tailed *K–S* test, $D_{(94)} = 0.122$, $p = 0.81$).

(Wassmann et al., 2006). In polar regions, the seasonal input of nutrient rich primary production originating from ice algae contributes an important seasonal input of organic matter to the benthos (Wassmann et al., 2011; Degen et al., 2016), impacting on biomass (Kêdra et al., 2013), growth (Blicher et al., 2010; Carroll et al., 2011a,b, 2014), benthic community physiology (Ambrose et al., 2006; Carroll and Peterson, 2013), and reproduction (Boetius et al., 2013). It has been consistently shown in polar environments that food has a greater impact on invertebrate physiology than temperature (Brockington and Clarke, 2001; Blicher et al., 2010), and can drive multi-decadal scale patterns in growth (Ambrose et al., 2006; Carroll et al., 2009) and recruitment (Skazina et al., 2013; Dayton et al., 2016). Associated with environmental forcing in the Arctic, there is expected to be a shift in the timings and quality of organic matter input to the benthos, from nutrient-rich ice algae to pelagic phytoplankton derived primary productivity (Arrigo and van Dijken, 2015), associated with thinner sea ice (Lange et al., 2019), and the transition to ice free conditions (Grebmeier et al., 2006; Leu et al., 2011; Polyakov et al., 2012a). Arctic phytoplankton assemblages may display resilience to ocean acidification through natural tolerances and intraspecific diversity (Hoppe et al., 2018), but the increasing unpredictability in quality of organic matter input impacts on the tight pelagic-benthic coupling which characterizes the Arctic (Tamelander et al., 2006; Wassmann et al., 2011; Kêdra et al., 2015). However, the observation that benthic species such as *Astarte* spp. and *Bathyarca glacialis* display feeding plasticity also ensures efficient use of available food input throughout the year (Gaillard et al., 2015; De Cesare et al., 2017), which may result in reproductive viability in otherwise unfavorable conditions.

Although gametogenesis may remain unaffected or mediated by food supply as a consequence of near future environmental change, the viability of fertilization and larval development under projected environmental conditions could still compromise successful recruitment (Dupont et al., 2010b; Kroeker et al., 2010; Albright, 2011). Fertilization across taxa has often shown negative responses to increasing carbon dioxide and temperature (e.g., Kurihara et al., 2007; Ericson et al., 2012; Guo et al., 2015; Graham et al., 2015), but results are not always consistent between species (Clark et al., 2009), populations (Thor et al., 2018), sexes (Verkaik et al., 2016), or individuals (Campbell et al., 2016; Boulais et al., 2017). Meanwhile "carry-over" effects and transgenerational plasticity may affect subsequent life cycle stages (Parker et al., 2011; Kong et al., 2019), shifting the development "bottleneck" to later stages, or forcing trade-offs with alternative reproductive traits such as fecundity or egg volume (Chakravarti et al., 2016). Larval development and early life history have also shown inconsistencies in their response to ocean acidification and increasing temperature. The Antarctic urchin *Sterechinus neumayeri* showed no differences in growth of reproductive tissue (Morley et al., 2016), or larval skeletal development (Clark et al., 2009) after exposure to ocean acidification and increased temperature, but a significant decrease in fertilization, developmental success, and increased developmental aberrations in alternative experiments have been recorded (Ericson et al., 2012; Byrne et al., 2013b). Larval type is also considered important, and planktotrophic larvae which are reliant on pelagic food are considered to be more susceptible than direct developing or non-feeding lecithotrophic larvae (Gutowska and Melzner, 2009; Dupont et al., 2010c; Gray et al., 2019). Consequently, biogeographical variations in larval responses to environmental change are likely to follow global and regional patterns of dominant larval types (Marshall et al., 2012). Here, both *A. crenata* and *B. glacialis* have oocyte sizes akin to non-feeding lecithotrophic or direct development (brooding) (Ockelmann, 1965) which is common in Polar species (Marshall et al., 2012), and suggests that food availability will have limited impact on larval development directly.

The lack of consistency between studies demonstrates the complex relationships between ocean acidification and temperature as synergistic stressors on individual reproductive performance (Byrne et al., 2013a; Harvey et al., 2013) and/or natural variations in tolerances within populations (Smith et al., 2019). Recruitment and recovery from disturbance in polar environments is often very slow (years – decades) (Barnes and Kukliński, 2005; Konar, 2013) although our knowledge of Arctic invertebrate reproductive biology remains limited (Kuklinski et al., 2013). The rapid rates of environmental change, however, may be further exacerbated by extreme longevity of organisms at high latitudes (Moss et al., 2016), To understand the effects of environmental change on reproductive ecology it will be important to consider all life history stages (Dupont et al., 2010a), and the role of population variability and plasticity as mechanisms of population resilience to environment change (Byrne et al., 2020). The role of changing food resources in determining reproductive viability in regions experiencing rapid change is presently under appreciated, but will be necessary to understand the links between the environment and reproductive/larval physiology (Goethel et al., 2017). The complex interactions between physiology, the environment, and climate change (Byrne et al., 2013a) will determine future population distributions and local extinction risks (Murdoch et al., 2020). We put forward, therefore, that holistic approaches including projected changes to regional food sources, are required to understand how future conditions may affect reproduction and modify interactions with whole animal physiological characteristics (Pörtner and Farrell, 2008; Dupont and Pörtner, 2013).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation. All histology image data are to be made openly available from the Discovery Metadata System (https://www.bas.ac.uk/project/dms/), a data catalogue hosted by The UK Polar Data Centre (UK PDC, https://www.bas.ac.uk/data/uk-pdc/).

AUTHOR CONTRIBUTIONS

AR and LG conceived the idea. AR conducted the laboratory work and image analysis and wrote the manuscript. JG and AR

analyzed the data and produced the figures. MS, LG, and JG reviewed and provided critical comments on the manuscript prior to submission. All of the authors have contributed to the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.576746/full#supplementary-material

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Supplemental information

Invariant gametogenic response of dominant infaunal bivalves from the Arctic under ambient and near-future climate change conditions

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Table S1. Summary of the station data for the collection of *A. crenata* and *B. glacialis* in the Barents Sea during Research Cruise JR16006 (2017) and JR17007 (2018), RRS James Clark Ross. Event numbers are from the ship log listed in the associated cruise reports (listed at end of supplementary material). All timings are in GMT.

Cruise	Event	Station	Date (ddmmyy)	Latitude (ºN)			Longitude (ºE)			Start time	Time at bottom	End time	Trawl duration (mins)	Depth (m)
				Start	Bottom	End	Start	Bottom	End					
JR16006	134	B13	170717	74.50878	74.50799	74.50219	29.98888	29.98968	29.99543	9.58	10.08	10.43	15	-
JR16006	135	B13	170717	74.50083	74.49983	74.49402	30.00348	30.00336	30.00338	11.00	11.12	11.47	15	359
JR16006	136	B13	170717	74.49341	74.49235	74.48652	30.00430	30.00335	30.00349	11.56	12.09	12.42	15	360
JR16006	137	B13	170717	74.49939	74.49899	74.49257	29.99641	29.99650	29.99644	13.07	13.12	13.53	15	363
JR17007	113	B17	180718	81.27922	81.27922	81.27979	29.34515	29.34460	29.26345	10:12	10:13	11:21	5	340
JR17007	115	B17	180718	81.27939	81.27938	81.27885	29.33728	29.33635	29.28820	12:58	13:00	13:46	15	344
JR17007	116	B17	180718	81.27882	81.27876	81.27847	29.28686	29.27970	29.24346	14:05	14:15	14:42	15	339
JR17007	118	B17	180718	81.28354	81.28332	81.28297	29.35273	29.33683	29.30954	16:15	16:32	16:51	15	339
JR17007	120	B17	180718	81.28397	81.28388	81.28342	29.34701	29.34098	29.30313	18:26	18:36	19:05	15	354
JR17007	121	B17	180718	81.28394	81.28310	81.27740	29.34459	29.34406	29.34019	19:36	19:46	20:14	15	350
JR17007	122	B17	180718	81.28475	81.28415	81.27814	29.33391	29.33843	29.38193	20:45	20:56	21:33	25	340
JR17007	172	B16	220718	80.11647	80.11562	80.10993	30.04722	30.05017	30.06896	17:39	17:48	18:27	15	282
JR17007	173	B16	220718	80.11593	80.11504	80.10932	30.04600	30.04885	30.06622	18:47	18:57	19:41	15	292
JR17007	174	B16	220718	80.11518	80.11409	80.10897	30.04508	30.04837	30.06422	19:56	20:06	20:48	15	292

Table S2. Biometric data for *A. crenata* and *B. glacialis* used for histological examination. Sex was derived from histology only, blanks were not selected for histology, '?' denotes no observed reproductive tissue. Shell morphology measured as described by Oliver et al. 2020. Shell length refers to maximum anterior – posterior length, shell height refers to dorsal-ventral length, tumitidy refers to maximum inflation of articulated valves.

Climate treatment	Species	Individual Number	Shell length (mm)	Shell height (mm)	Tumidity (mm)	Weight (g)	Tissue Weight (g)	Sex (derived from histology)
Ambient	*A. crenata*	1	26.08	20.62	11.70	4.7912	0.5243	
Ambient	*A. crenata*	2	24.23	20.64	11.81	4.8780	0.4968	
Ambient	*A. crenata*	3	30.01	23.47	13.26	8.0734	0.9910	
Ambient	*A. crenata*	4	24.85	19.43	10.72	3.8639	0.4726	male
Ambient	*A. crenata*	5	27.23	22.78	12.55	5.8938	0.9295	female
Ambient	*A. crenata*	6	26.74	21.82	12.85	6.7128	0.7903	
Ambient	*A. crenata*	7	31.13	24.80	14.85	9.2388	0.9954	
Ambient	*A. crenata*	8	28.25	23.13	12.16	5.7086	0.7991	male
Ambient	*A. crenata*	9	22.33	20.50	12.24	4.8359	0.4657	male
Ambient	*A. crenata*	10	24.83	18.99	13.10	5.0705	0.5133	female
Ambient	*A. crenata*	11	30.90	24.58	12.70	7.2276	0.9488	female
Ambient	*A. crenata*	12	24.19	18.70	12.00	3.9199	0.4781	female
Ambient	*A. crenata*	13	28.07	23.48	11.73	6.2795	0.8536	female
Ambient	*A. crenata*	14	28.31	23.95	13.26	7.2243	0.9377	
Ambient	*A. crenata*	15	22.26	19.32	11.77	4.1813	0.4110	
Ambient	*A. crenata*	16	23.76	19.71	13.62	5.3101	0.5551	
Ambient	*A. crenata*	17	28.13	21.51	12.19	6.1445	0.8262	female
Ambient	*A. crenata*	18	24.59	19.30	11.62	5.0616	0.6066	male
Ambient	*A. crenata*	19	30.56	25.38	13.24	8.5249	1.0709	male
Ambient	*A. crenata*	20	25.27	19.65	11.59	4.6062	0.5611	female
Ambient	*A. crenata*	21	25.86	21.60	11.32	5.2941	0.6657	male
Ambient	*A. crenata*	22	24.70	21.12	11.55	4.7138	0.5445	male
Ambient	*A. crenata*	23	24.23	21.75	12.25	5.2979	0.5750	
Ambient	*A. crenata*	24	22.45	18.74	10.62	3.5231	0.4338	male
Ambient	*A. crenata*	25	26.78	22.85	13.06	6.8733	1.0372	male
Ambient	*A. crenata*	26	25.89	21.70	12.95	5.7507	0.9381	
Ambient	*A. crenata*	27	21.86	17.04	10.51	3.0989	0.6022	female
Ambient	*A. crenata*	28	24.04	19.93	13.11	5.1734	0.4225	male
Ambient	*A. crenata*	29	22.41	18.16	11.81	3.7170	0.4600	
Ambient	*A. crenata*	30	26.89	21.65	13.11	6.5487	0.7703	female
Future	*A. crenata*	31	26.24	21.42	11.24	5.1028	0.5584	
Future	*A. crenata*	32	24.73	20.75	12.25	4.7755	0.5865	female
Future	*A. crenata*	33	27.18	25.47	11.92	6.1647	0.7505	
Future	*A. crenata*	34	22.27	18.16	13.17	4.5070	0.4094	
Future	*A. crenata*	35	31.73	25.77	13.05	8.2354	1.1233	male
Future	*A. crenata*	36	25.45	19.73	12.14	4.8464	0.3826	male
Future	*A. crenata*	37	25.52	20.65	11.57	5.1645	0.5678	male

Future	*A. crenata*	38	30.05	22.16	12.16	6.2068	0.9342	female
Future	*A. crenata*	40	24.73	19.77	11.64	4.8244	0.5613	
Future	*A. crenata*	41	24.28	19.46	11.37	4.2691	0.4995	female
Future	*A. crenata*	42	23.68	18.63	10.78	3.7062	0.3881	male
Future	*A. crenata*	43	24.69	19.06	11.16	4.5022	0.4682	female
Future	*A. crenata*	44	27.21	21.72	11.31	4.9745	0.5848	male
Future	*A. crenata*	45	24.11	20.34	10.61	4.2926	0.5481	male
Future	*A. crenata*	46	21.22	18.76	10.80	3.3664	0.4090	
Future	*A. crenata*	47	26.17	21.13	11.54	4.4923	0.4912	male
Future	*A. crenata*	48	25.91	19.91	12.33	5.2749	0.7398	male
Future	*A. crenata*	49	30.93	25.21	14.60	8.8061	1.0533	female
Future	*A. crenata*	50	28.81	25.01	11.98	6.8988	0.8043	female
Future	*A. crenata*	51	23.51	17.73	10.41	3.6716	0.4810	male
Future	*A. crenata*	52	27.15	21.75	12.06	6.1726	0.6944	
Future	*A. crenata*	53	28.22	22.19	13.51	6.7903	0.7383	male
Future	*A. crenata*	54	25.86	20.70	11.44	5.0540	0.5501	male
Future	*A. crenata*	55	25.31	20.52	12.02	5.3860	0.5247	
Future	*A. crenata*	56	25.99	21.76	11.65	5.0335	0.7250	?
Future	*A. crenata*	57	22.95	19.43	9.73	3.5654	0.4188	
Future	*A. crenata*	58	26.64	19.63	12.80	5.1186	0.8253	
Future	*A. crenata*	59	29.83	23.60	11.77	6.5804	0.9868	
Future	*A. crenata*	60	26.21	20.83	11.87	5.5369	0.6253	female
Ambient	*B. glacialis*	1	18.94	14.44	9.28	1.4553	0.5051	male
Ambient	*B. glacialis*	2	21.77	15.17	10.16	1.6878	0.3563	male
Ambient	*B. glacialis*	3	24.33	17.18	10.24	2.0013	0.5293	female
Ambient	*B. glacialis*	4	21.95	16.04	10.05	1.9207	0.7017	female
Ambient	*B. glacialis*	5	20.61	15.18	9.53	1.2287	0.2934	male
Ambient	*B. glacialis*	6	22.88	16.76	10.94	2.1913	0.6582	male
Ambient	*B. glacialis*	7	19.7	15.51	10.49	1.6905	0.3804	female
Ambient	*B. glacialis*	8	20.02	14.21	8.67	1.3375	0.3883	female
Ambient	*B. glacialis*	9	22.66	16.1	9.91	1.702	0.4128	male
Ambient	*B. glacialis*	10	20.92	14.93	8.97	1.394	0.5566	male
Ambient	*B. glacialis*	11	21.45	16.23	9.67	1.180	0.518	female
Ambient	*B. glacialis*	12	22.22	15.65	10.25	1.7629	0.5087	male
Ambient	*B. glacialis*	13	22.02	17.72	10.82	1.5811	0.4957	male
Ambient	*B. glacialis*	14	19.94	15.2	8.86	1.3373	0.3123	female
Ambient	*B. glacialis*	15	22.78	17.29	10.15	1.9303	0.6623	male
Ambient	*B. glacialis*	16	20.72	15.04	9.14	1.149	0.523	female
Ambient	*B. glacialis*	17	21.09	15.83	9.72	1.15921	0.637	female
Ambient	*B. glacialis*	18	21.42	16.04	9.71	1.6733	0.601	male
Ambient	*B. glacialis*	19	21.21	15.3	9.46	1.4968	0.5244	male
Ambient	*B. glacialis*	20	21.83	15.1	9.19	1.4901	0.4787	female
Ambient	*B. glacialis*	21	20.77	15.5	9.92	1.391	0.6635	female
Ambient	*B. glacialis*	22	22.18	17.46	10.62	1.9518	0.5913	male
Ambient	*B. glacialis*	23	21.52	16.35	9.39	1.5997	0.5277	male
Ambient	*B. glacialis*	24	21.2	15.92	8.61	1.5003	0.5543	male

Table S3. Summary of sediment particle size statistics given by the default GRADISTAT output (Blott & Pye, 2001). Mean, sorting, skewness, kurtosis, the percentage of sample less than 63 μm and total organic carbon are presented for (a) 2017, cruise JCR16006 and (b) 2018, cruise JCR17007. Superscripts provide descriptive terminology as outlined by Blott & Pye (2001). **Mean, $\bar{x}$:** fs, fine silt; ms, medium silt; cs, coarse silt; vcs, very coarse silt. **Sorting, σ:** ps, poorly sorted; vps, very poorly sorted. **Skewness, *Sk*:** sy, symmetrical; vfsk, very fine skewed; fsk, fine skewed; csk, coarse skewed. **Kurtosis, *K*:** mk, mesokurtic; lk, leptokurtic; pk, platykurtic. Data from Solan et al. 2020, obtained on the same research cruise and station occupancy date.

Station	Event number	Mean ($\bar{x}$, μm)	Sorting (σ, μm)	Skewness (Sk, μm)	Kurtosis (K, μm)	Sample <63 μm (%)	Total organic carbon (TOC, %)	Sediment name
(a) JCR16006								
B13	331	22.27^{ms}	27.28^{ps}	2.080^{sy}	7.131^{mk}	90.902	6.777	Medium silt
B13	332	24.47^{ms}	35.53^{ps}	2.993^{sy}	14.17^{mk}	89.783	7.205	Very fine sandy medium silt
B13	333	40.47^{cs}	66.83^{vps}	3.426^{sy}	17.12^{mk}	82.298	6.229	Very fine sandy coarse silt
B13	334	25.12^{ms}	29.33^{ps}	1.743^{sy}	5.276^{mk}	88.010	6.748	Very fine sandy coarse silt
(b) JCR17007								
B16	189	33.29^{ms}	69.49^{ps}	4.736^{sy}	29.43^{lk}	89.361	5.643	Very fine sandy medium silt
B16	190	32.66^{ms}	64.63^{ps}	4.509^{sy}	27.51^{lk}	88.799	6.229	Very fine sandy medium silt
B16	191	51.71^{cs}	102.0^{vps}	3.276^{csk}	14.27^{lk}	82.795	6.231	Very fine sandy medium silt
B16	192	40.31^{ms}	91.13^{ps}	4.174^{csk}	21.56^{lk}	87.475	6.024	Very fine sandy medium silt
B17	134	28.46^{ms}	55.14^{ps}	5.079^{sy}	34.27^{mk}	91.254	6.250	Medium silt
B17	135	22.01^{ms}	29.75^{ps}	3.682^{sy}	20.59^{mk}	94.024	6.101	Medium silt
B17	136	23.49^{ms}	40.14^{ps}	5.252^{sy}	39.00^{mk}	93.434	6.209	Medium silt
B17	137	32.07^{ms}	50.59^{ps}	4.045^{sy}	23.70^{mk}	88.540	6.271	Very fine sandy coarse silt

Table S4. Known egg sizes and locations of i) Astartidae; ii) *Astarte crenata* in this study; iii) *Bathyarca glacialis* from this study

	Species	Egg size	Mean egg size	Location	Reference
i)	*Astarte borealis*	150 - 200 µm	-	Greenland	Thorsen 1936
	Astarte elliptica	150 - 200 µm	-	Baltic Sea	Von Oertzen 1972
	Astarte sulcata	150 – 200 µm	-	North Atlantic	Saleuddin 1964
	Digitaria digitaria	150 – 180 µm	-	Strait of Gibraltar	Marina et al. 2020
ii)	*Astarte crenata*	36.23 – 281.21 µm	129.33 µm ± 38.71 SD, n = 1200	Barents Sea	Personal observation
	Astarte crenata	46.96 – 185.08 µm	122.61 µm ± 24.01 SD, n = 500	Ambient Treatment	This study
	Astarte crenata	44.61 – 181.93 µm	122.48 µm ± 22.84 SD, n = 500	Future Treatment	This Study
iii)	*Bathyarca glacialis*	39.60 – 144.77 µm	96.77 µm ± 14.36 SD, n = 500	Ambient Treatment	This Study
	Bathyarca glacialis	35.07 – 144.90 µm	95.03 µm ± 18.57 SD, n = 500	Future Treatment	This Study

Figure S1. Cumulative sediment particle size distributions (n = 4) for stations (a) B13 in 2017, (b) B16 in 2018 and (c) B17 in 2018. Data from Solan et al. 2020, obtained on the same research cruise and station occupancy date.

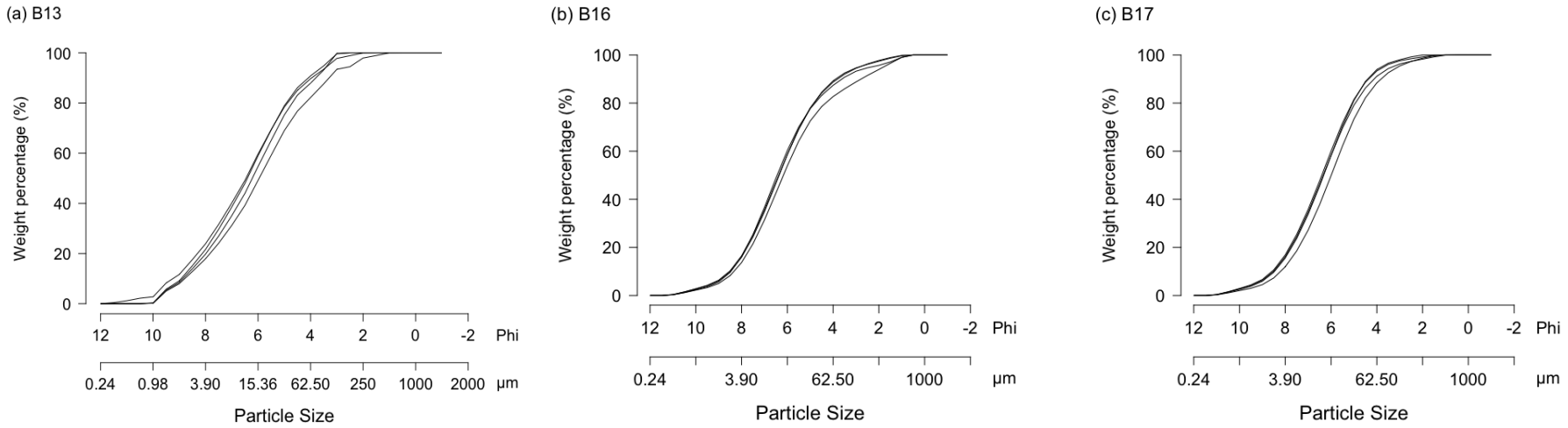
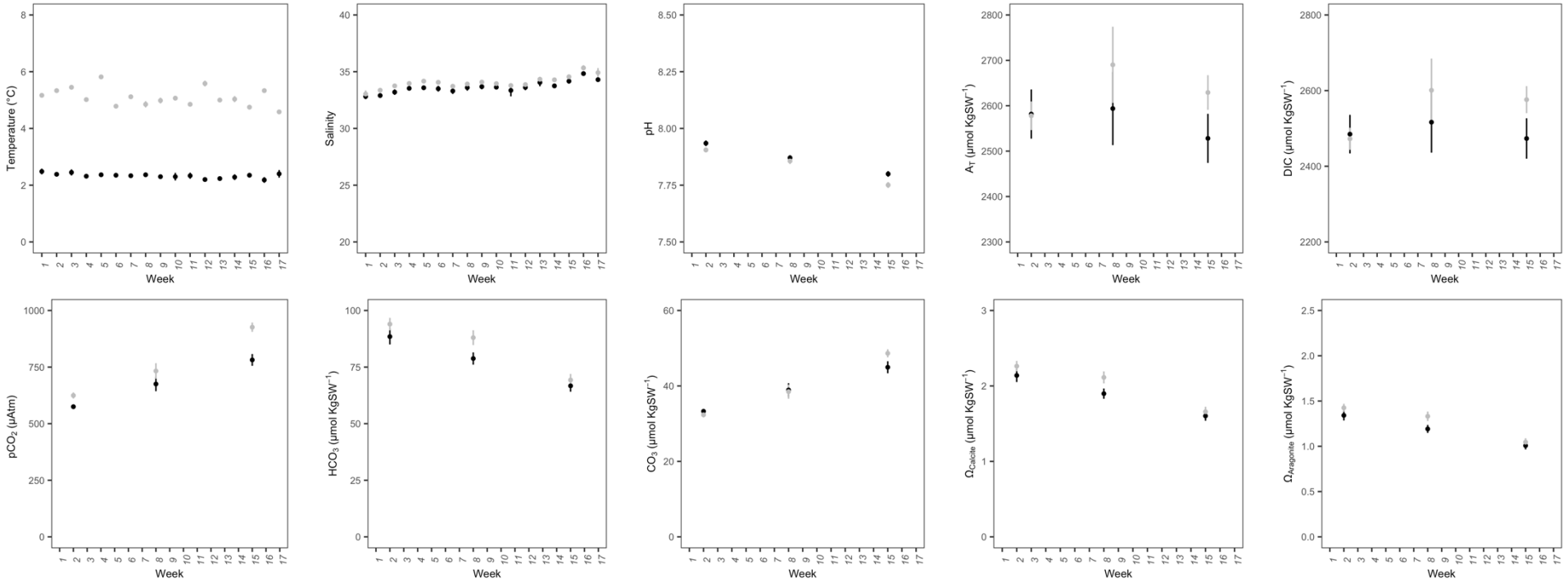


Figure S2. Summary of periodic seawater measurements in aquaria under ambient (black) and near-future (grey) conditions for (a) *B. glacialis* and (b) *A. crenata*. Temperature (°C), Salinity, pH_{NBS} and total alkalinity (AT, µmol $kgSW^{-1}$) were measured directly from each aquarium and were used to calculate dissolved organic carbon (DIC, µmol $kgSW^{-1}$), pCO_2^{SW} (µAtm), saturation states for calcite (ΩCalcite) and aragonite (ΩAragonite), bicarbonate (HCO_3, µmol $kgSW^{-1}$) and carbonate (CO_3, µmol kgSW-1) using CO_2calc (Robbins et al. 2010). Error bars represent standard deviation.

(a)



(b)

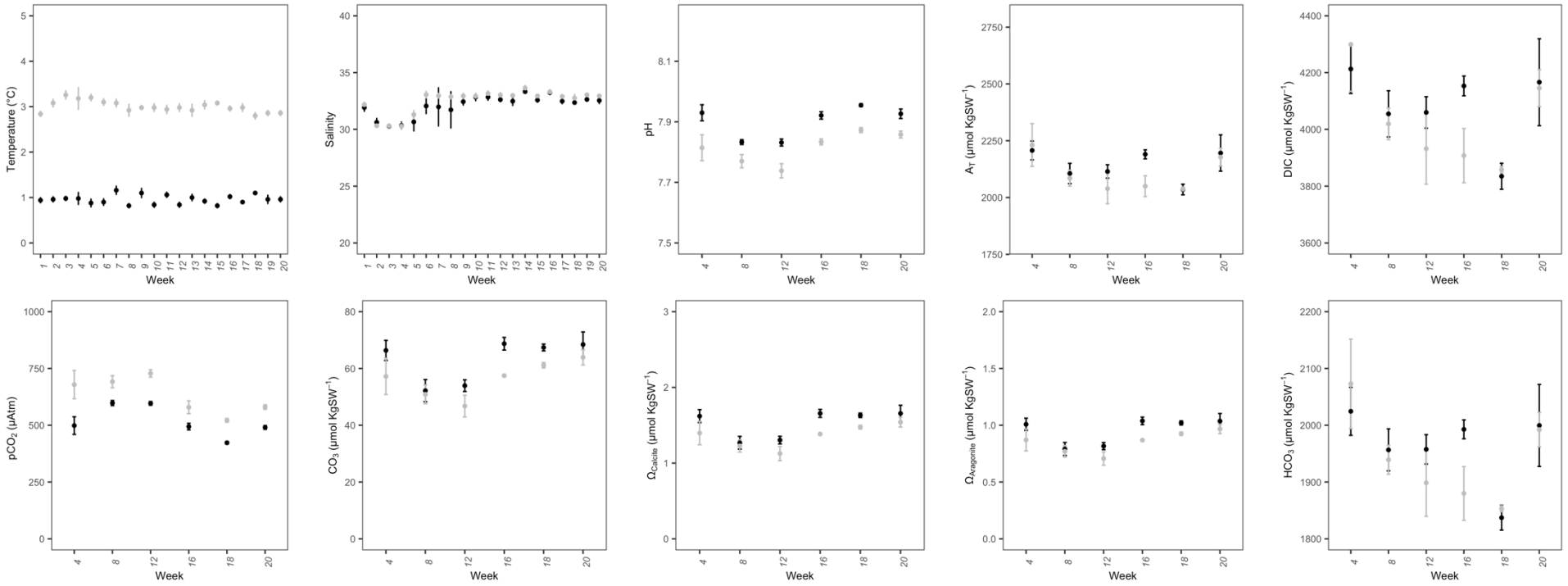
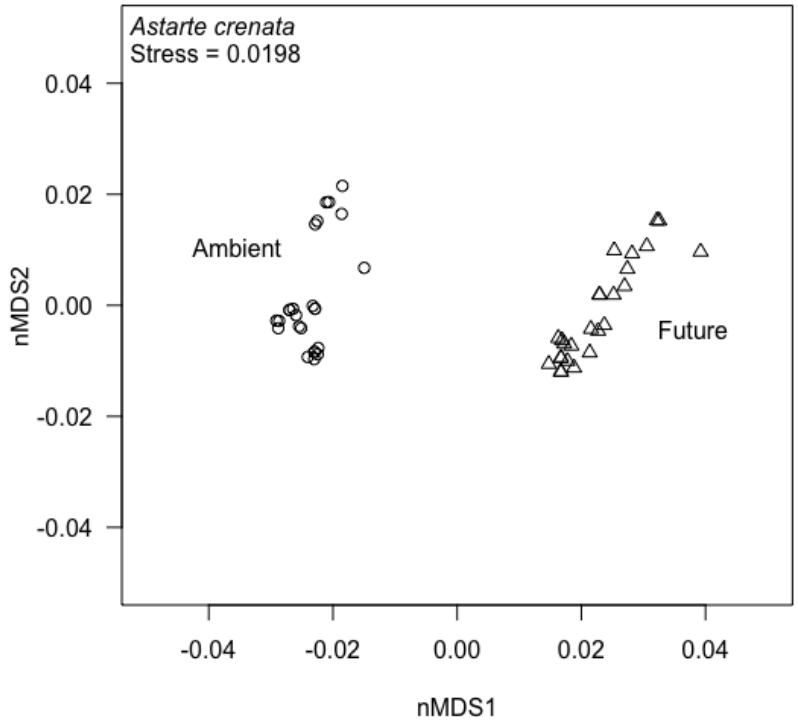

Temperature (°C)
Salinity
pH
A_T (µmol KgSW^{-1})
DIC (µmol KgSW^{-1})
pCO_2 (µAtm)
CO_3 (µmol KgSW^{-1})
$\Omega_{Calcite}$ (µmol KgSW^{-1})
$\Omega_{Aragonite}$ (µmol KgSW^{-1})
HCO_3 (µmol KgSW^{-1})
Week

Figure S3. Classification of the experimental conditions for (a) *Astarte crenata* and (b) *Bathyarca glacialis* from the Barents Sea under ambient (open circles; 1 - 2°C, ~400 ppm [CO_2]) and near-future (open triangles; 3 - 5°C, ~550 ppm [CO_2]) scenarios shows a clear separation between treatment groups. Non-metric two-dimensional (nMDS) representations of euclidean similarity matrices based on 10 water and carbonate chemistry parameters (temperature, salinity, pH, total alkalinity, HCO_3, CO_3, pCO_2, calcite, aragonite and DIC) are presented. Dimensionality representation stress values (k=2) are (a) 0.0080 and (b) 0.0198.

(a)



(b)

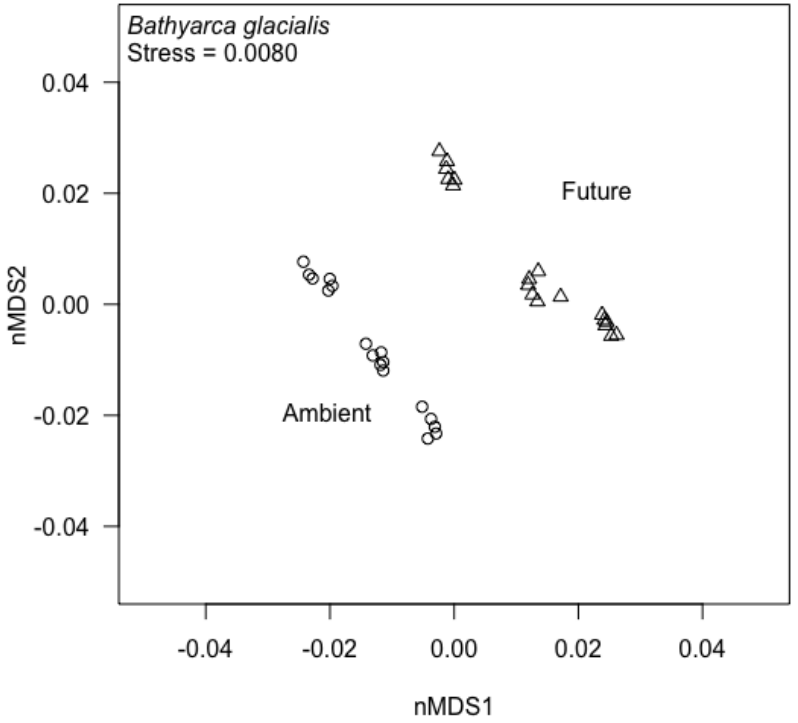


Figure S4. Individual oocyte size frequency histograms for *Astarte crenata* maintained in ambient (top) and future (bottom) conditions. Statistically significant associations were found between individual females and oocyte size frequencies in each treatment (Ambient $x^2 = 143.17$, d.f. = 28, $p < 0.0001$; Future $x^2 = 97.263$, d.f. = 24, $p < 0.0001$).

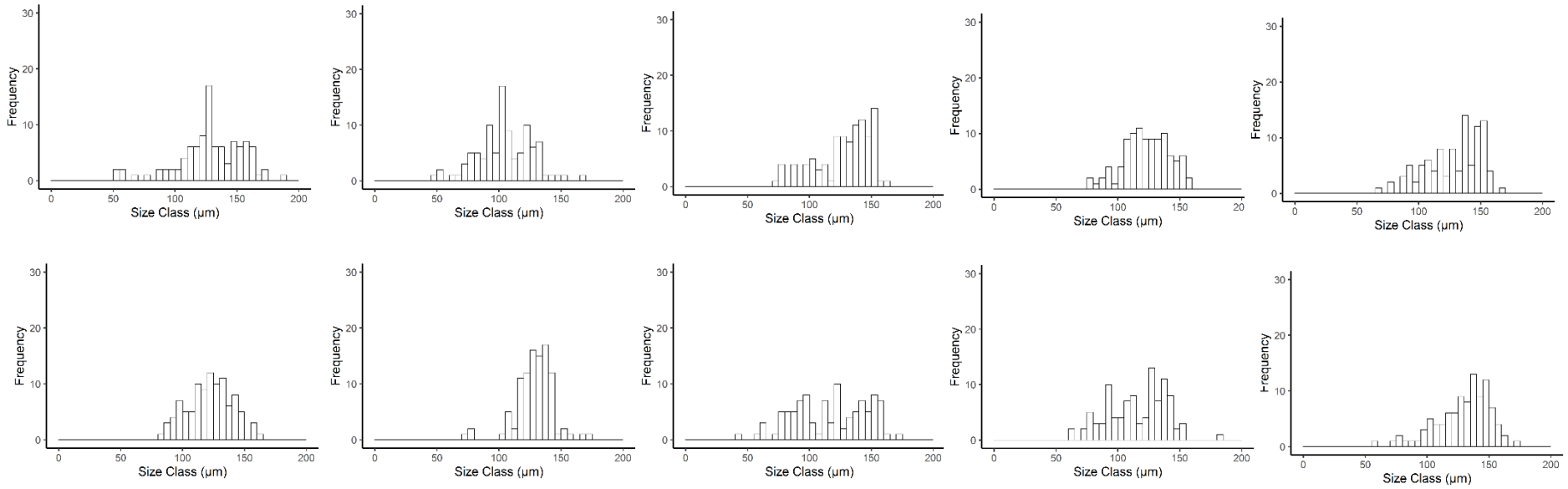
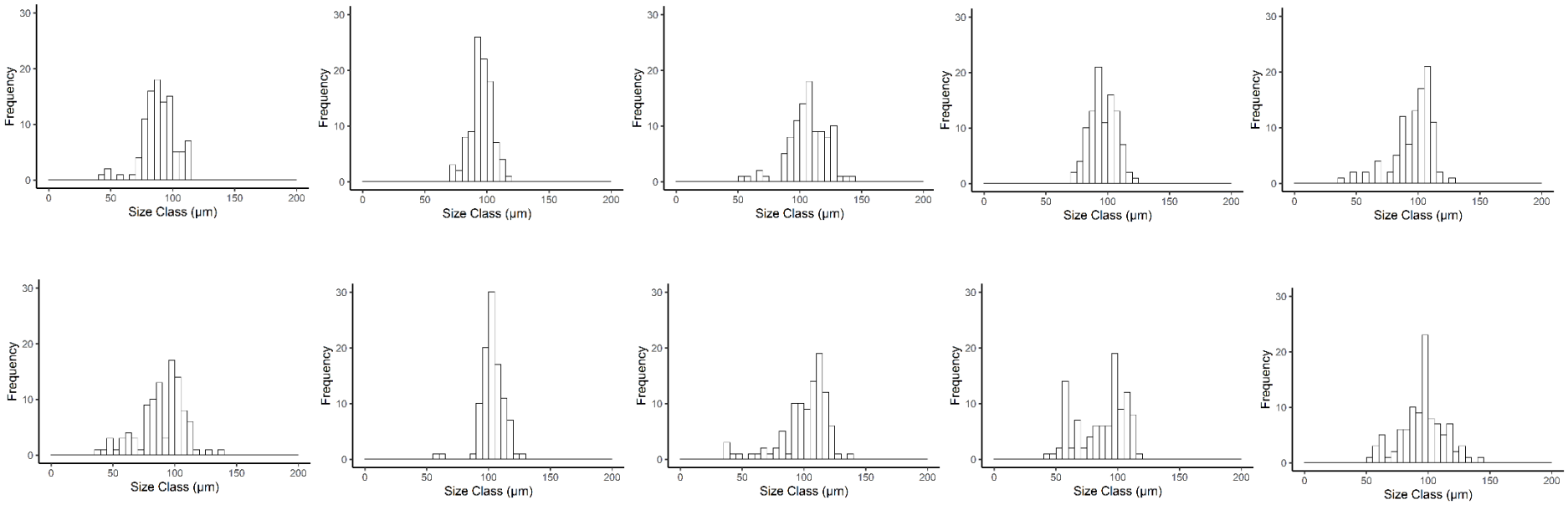


Figure S5. Individual oocyte size frequency histograms for *Bathyarca glacialis* maintained in ambient (top) and future (bottom) conditions. Statistically significant associates were found between individual females in each treatment (Ambient $x^2 = 172.86$, d.f. = 20, $p < 0.0001$; Future $x^2 = 119.43$, d.f. = 20, $p < 0.0001$).



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Cruise reports for this research programme can be obtained from the British Oceanographic Data Centre at:

https://www.bodc.ac.uk/resources/inventories/cruise_inventory/results/

Cottier FR. 2017 RRS James Clark Ross cruise, JR16006

Solan M. 2018 RRS James Clark Ross cruise, JR17007

Barnes D. 2019 RRS James Clark Ross cruise, JR18006 (not included in the present contribution, but listed here as it forms the third and final cruise of this research programme)

Ends.